with the upperside markings showing through, and with a well-defined central whitish band becoming more or less merged with the ground-colour at anal angle.

Expanse 82 mm.

Hab. Haiti, no precise locality.

Type in Coll. Joicey.

Anaea xenocrates punctimarginale, subsp. n.

♂. Differs from *xenocrates xenocrates* from Bolivia in the fore wing by having no blue scaling at tornus and in the blue subapical spots being widely separated and showing no tendency to unite inwards. Hind wing with a series of rather small triangular blue marginal spots, not a band as in the Bolivian form.

♀. Shows much less difference from type-form. The margin of hind wing is yellow banded as in the ♀ from Bolivia. There is an extra yellow spot between veins 3, 4, smaller than that between veins 2, 3.

Expanse 82 mm.

Hab. French Guiana, St. Jean de Maroni.

1 ♂, 1 ♀.

Type in Coll. Joicey.

The occurrence in French Guiana of a species only known hitherto from Bolivia and the Upper Amazons (Pebas) is strange, and at first suggests specific difference and not subspecific. But the species is rare, the ♀ exceedingly so, and its range may lie across the interior of Brazil where it could easily remain undetected. The species has been chiefly known from Eastern Bolivia, but the few specimens known from Pebas belong to the same form with a blue marginal hind-wing band in the ♂.

XXVI.—*Observations on the Genus* Lysorophus, *Cope.* By Robert Broom. *With a Note*, by Prof. W. J. Sollas.

So much has already been written about this little vertebrate by Broili, Case, v. Huene, Moodie, Finney, and Williston that it might seem doubtful wisdom to add another paper to the already extensive literature, and more especially as my observations are on specimens already carefully examined by Case and v. Huene; but when one considers that *Lysorophus* is the most remarkable land vertebrate that has been discovered for many years, and that opinions not only differ as to its affinities but also as to the interpretation of a number of the cranial elements, a further review of even the present evidences seems justifiable.

There is no lack of material. The Chicago Museum has 200 nodules, each containing much of the skeleton of a specimen: the American Museum, New York, also has many nodules, and in the American Museum nine skulls have been chiselled out, one or two in very good condition. In Tübingen there are 24 skulls, and at Munich a considerable number more.

As the extensive literature has been reviewed by Williston and others, it will be unnecessary to enter into this in detail. To Broili we owe the first really good figures of the skull, but there are one or two points in his interpretation that I, in common with all later writers, do not accept, and from his conclusion as to the affinities of the genus I also differ.

Case gives a brief description of the more conspicuous elements of the skull, and reproduces Broili's and Williston's figures. As these two figures differ in a number of points, one could have wished that Case had given an original figure of his own interpretation, and his description, while pointing out the different views, does little to clear up the matter.

Williston gives us clear definite views as to the structure of the skull and skeleton, and equally clear opinions as to the affinities of the genus.

Von Huene, the latest worker on the genus, has just issued a paper on *Lysorophus* in the 'Anatomischer Anzeiger,' and another paper is in the press describing the specimens in the American Museum. Though these two papers are appearing in the same year, I believe that the one in the 'Anatomischer Anzeiger' to be the later. On one or two points the opinions expressed differ in the two, and it is therefore well to know which is the latest. Von Huene has figured a number of the better skulls in the American Museum, and gives us clear opinions not only on the structure, but also on the affinites of the genus.

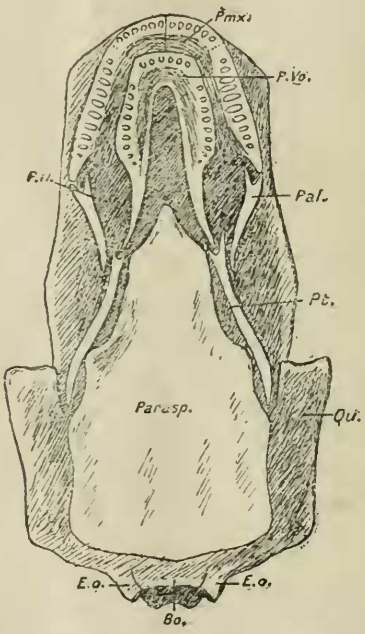
The skulls in the American Museum, though comparatively few in number, are mostly well preserved, and there is scarcely a point in the structure that cannot be made out in one or other.

The best figures published of the top of the skull are those of Broili and Williston, and they differ, apart from interpretations, only in the relative width of the nasal region. While neither is altogether correct, a composite of the two would give the truth. The difference arises from the peculiar state of affairs in front of the prefrontal. Broili correctly recognises a round opening here which he regards as the nostril. It is also shown in Williston's specimen. The most natural conclusion would seem to be that this is

the nostril, but two of the American Museum specimens seem to indicate that the opening extends somewhat inwards and forwards, and one would like to see a specimen showing the perfect snout to feel quite sure that this opening is the nasal opening and not perhaps also an opening for some sensory organ.

There is a small premaxilla—possibly toothed. It is figured by v. Huene. The maxilla is slender and carries about ten teeth. Its posterior end articulates, I believe, with the palatine. It forms the floor of the nasal opening

Fig. 1.



Restoration of the underside of skull of *Lysorophus tricarinatus*, Cope, × 5.

and perhaps its posterior border. The doubt lies in the fact that in the specimens it is impossible to be quite sure whether the bridge of bone which connects the prefrontal with the maxilla is a part of the prefrontal or a part of the maxilla or a small independent bone.

One specimen shows most of the palate. The bones are a little crushed and fractured, and the interpretation I give is made with some hesitation (fig. 1). Von Huene figures the specimen, but his interpretation differs somewhat from mine,

which agrees pretty closely with Broili's. I consider v. Huene in error in regarding that there are "two large, elongate internal nares, separated by a narrow bridge." The large supposed left choana of v. Huene I regard as the median vacuity between the prevomers, and the narrow bridge as the right prevomer. The figure I give will show how I interpret the palatal structures. The prevomers form a horseshoe-like arrangement with posterior processes passing back to the parasphenoid and apparently articulating with the pterygoids. The teeth on the prevomers are well shown in this specimen. In front there are about 6 and about 8 on each side. The palatines are delicate bones extending from the maxillæ to the pterygoids. Between the palatines and prevomers are, I believe, the internal nares. The pterygoids extend back as rather delicate bones to meet the quadrates. The parasphenoid is a very large bone, which forms nearly the whole of the base of the posterior two-thirds of the skull. The supposed suture figured by v. Huene between the parasphenoid and the basisphenoid is, I think, a fracture merely.

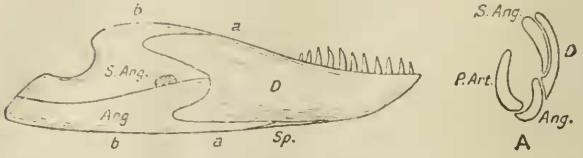
The figure I give of a transverse section of the skull (fig. 3) shows the relations of the pterygoid to the parasphenoid, and also the elements of the back of the mandible.

In Broili's figure A of the side view of the skull, there are seen in the orbital region some deep-seated elements. These are also shown in two of the American Museum specimens. In what might be regarded as the sphenethmoid region there appear to be three elements with a deep posterior notch. In one of the New York specimens an almost exactly similar appearance is shown, and further back an elongated element very like an epipterygoid in appearance. Though these elements have been seen by Broili, neither he nor anyone else appears to have expressed any opinion as to what they were. After considering many possibilities I have come to the conclusion that they are ossifications or calcifications in the cartilaginous brain-case. The anterior elements look as if separated by sutures, but, whereas all true sutures in the skull and even cracks are filled with the red clayey matrix, these divisions are formed of clear calcite which probably indicates that they were originally formed by hyaline cartilage. Further, in a second specimen the ossification appears to be entire. The posterior narrow vertical element is also, in my opinion, an ossification of the cranial cartilage. It certainly has much superficial resemblance to a reptilian epipterygoid. It articulates with the parietal above and passes down to at least near to the pterygoid. It thus answers in position to the epipterygoid.

But though in front it has a smooth edge the posterior edge is irregular, as if indicating an ossification in cartilage. The anterior ossification or ossifications probably correspond to the sphenethmoid of *Siredon* or the frog, and the posterior to the ossification seen in Dinosaurs, Crocodiles, and birds, and usually, but I think wrongly, called alisphenoid.

The quadrate is large and its upper half is largely hidden by the squamosal. There need not, I think, be the slightest

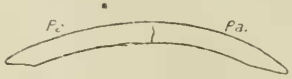
Fig. 2.

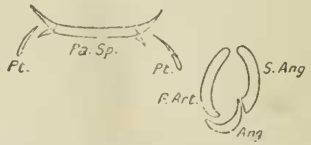


Lower jaw of *Lysorophus tricarinatus*, Cope, × 5. **A** represents a section at *a a*.

Ang., angular; *D*, dentary; *P.Art.*, prearticular; *S.Ang.*, surangular.

Fig. 3.





Section across skull and jaw of *Lysorophus tricarinatus*, Cope, × 5. The section of the lower jaw is near the point indicated by *b b* in the figure of the jaw. The outer corners of the parasphenoid are separated by cracks or sutures. They are believed to be parts of the parasphenoid.

Ang., angular; *Pa.*, parietal; *Pa.Sp.*, parasphenoid; *P.Art.*, prearticular; *Pt.*, pterygoid; *S.Ang.*, surangular.

doubt about this bone being the squamosal—the view also held by Williston and v. Huene.

The occiput has recently been figured by v. Huene from one of the American Museum specimens and also from one of the Tübingen specimens. His drawing of the American Museum specimen is not in my opinion quite accurate, the American specimen agreeing closely with his figure of the Tübingen specimen. The main difference between the two

is that in the drawing of the American specimen the exoccipital is represented as very small. This is, I think, wrong, the exoccipital being large, as represented in the drawing of the Tübingen specimen. The drawing v. Huene gives of the occipital condyle is thoroughly satisfactory, showing that the articulation is as much basi- as exoccipital. Von Huene's identifications of the fenestra ovalis and foramen for the vagus are probably correct.

The large bone situated by the sides of the supraoccipital has been very variously identified. By Broili and Case they have been called squamosals, by Williston epiotics, and by v. Huene supratemporals. That they cannot be squamosals requires no argument, the undoubted squamosals lying in front. Nor can they, I think, be regarded as supratemporals. From their being quite behind the parietals, and at the sides of the supraoccipital and far behind the jaw, it is very doubtful if they in any way roof the temporal region. They may be epiotics, but we do not know any forms in which epiotics take up this position. They further appear to overlap the supraoccipital, and to be thus membrane bones. It seems to me that they, however, answer all the requirements of the tabulares. They lie on the outer part of the paroccipitals, are behind the parietals, and articulate with both the parietals and squamosals, and to form the upper lateral parts of the occiput.

The lower jaw has never been fully described. Von Huene figures one of the specimens in the American Museum, but with one or two of his interpretations I do not agree. He has also examined some jaws in the Tübingen Museum, but they have apparently not yielded any fresh light. The American Museum specimen, no. 4761, shows something of the jaw, but not nearly so much as two other specimens not numbered. Between these three specimens practically all details can be made out (fig. 2).

The dentary forms about two-thirds of the jaw. It comes to a sharp point in front and forms with its neighbour a short feeble symphysis. It articulates on the outer side behind with the surangular and angular. The splenial is a small bone lying on the inside of the lower part of the dentary just behind the symphysis. It forms the lower margin of the jaw in this region. The angular forms nearly the whole of the lower border of the jaw, passing in front between the dentary and the splenial. From two of the American Museum specimens I incline to differ from v. Huene, and believe that the splenial does not form part

of the symphysis. The surangular forms the upper half of the back of the jaw as indicated in the figure. Von Huene is, I think, in error in regarding the large opening in the side of the jaw in specimen 4716 as natural. Only a small part is, I believe, a natural opening, the rest due to faulty preparation. In other specimens the lateral opening is quite small, as indicated in the figure. I find no evidence of a coronoid element. Inside the jaw is a large prearticular. The articular is evidently quite small, and possibly cartilaginous.

Though the structure of the skull of *Lysorophus* may now be said to be pretty well known, there is still some little doubt as to the affinities. *Lysorophus* agrees closely with no known animal, recent or extinct. With Williston I agree in holding that *Lysorophus* is not a reptile. All known reptiles are either Cotylosaurs or are manifestly derived from Cotylosaurian ancestors, but *Lysorophus* is neither a Cotylosaur nor can it have been derived from a Cotylosaur. The supposed reptilian resemblances are entirely fallacious. Von Huene in his recent paper, though correctly figuring and describing the occipital condyle, says: "this condyle is intermediate between the true reptilian condyle and the true amphibian condyle . . . . The structure of the condyle shows a great resemblance to that of the Theromorphs and of Turtles." In Theromorphs and Turtles the condyle is a tripartite condyle, of which the upper two-thirds are formed by the exoccipitals and the lower third by the basioccipital. In most Chelonians and Theromorphs the exoccipitals come close together, and the basioccipital is squeezed out from the foramen magnum. In all generalised forms the condyle is a projecting rounded structure which articulates with the arches of the atlas and with the intercentrum. In *Lysorophus* the whole articulation is with the centrum of the atlas, which fits close into the broad hollowed out surface formed by the basi- and exoccipitals. The presence of a large articular surface on the basioccipital seems at first sight to be a non-Amphibian character, but, as Watson has recently pointed out, this is the primitive Amphibian condition. The early Stegocephalians of the Lower Carboniferous, such as *Pteroplax*, have the basioccipital forming practically the whole of the articulation, the exoccipitals only very gradually in later forms taking the place of the basioccipital. So that, so far from the occipital condyle of *Lysorophus* indicating any reptilian affinities, it is really in a more primitive condition than is found in any other Permian or later Amphibian.

Doubtless Williston is right in regarding *Lysorophus* as a mud-borrowing animal, and many of its specialisations are due to this habit, such as the greatly elongated snake-like body with very numerous vertebræ, great reduction of the limbs, relatively small size of skull, loss of the arches, and advanced position of the quadrate. And the somewhat similar characters, acquired by convergence in other groups which have similar habits, have given rise to some striking superficial resemblances to *Lysorophus* in the Gymnophiona, the Amphisbænans, and the Typhlopidæ.

But, apart from all modifications in *Lysorophus* due to a burrowing habit, the skull is undoubtedly fundamentally an Amphibian skull, and the only known Amphibia, recent or extinct, with which it seems at all allied are the Urodela, and, more remotely, the Anura and the Gymnophiona.

Note by Prof. W. J. Sollas.

Some years ago Dr. Broom obtained, through the kindness of Dr. Matthew, two specimens of *Lysorophus*, and these he presented to me for investigation by serial sections; at the same time he made a most generous addition to this gift by placing in my hands, to dispose of as I thought fit, a paper embodying the important conclusions to which he had been led from his study of the specimens in American museums.

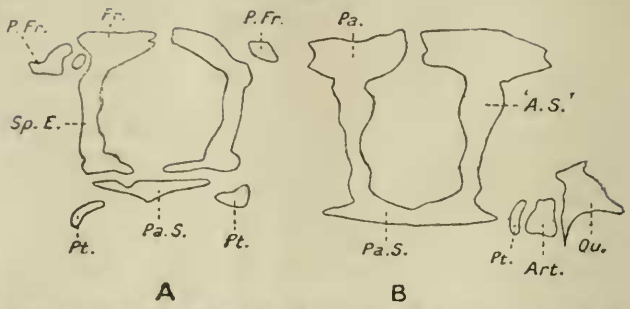
My own study is now completed, and I hope soon to give a full and exact account of the structure of the skull in all its details. This will confirm all the more important conclusions of Dr. Broom, and in justice to him I can no longer withhold from publication the paper which he entrusted to me in 1914.

One or two minor emendations ought, perhaps, to be made. Thus, the vacuity between the vomers, as it is represented in fig. 1, does not really exist; these bones are without thickened margins and meet in the middle line; and, again, the articulare of the lower jaw is a comparatively large and important bone.

On the other hand, there can be no doubt that the cranial walls include, as Dr. Broom suggests, a large "sphenethmoid" and "alisphenoids." These are shown in section in the accompanying figures (figs. 4 & 5).

The whole anatomy of the skull recalls in a striking manner that of *Siren* or *Menopomus*, and to my mind *Lysorophus* is without doubt an ancestral Urodele. It presents some remarkably interesting primitive characters.

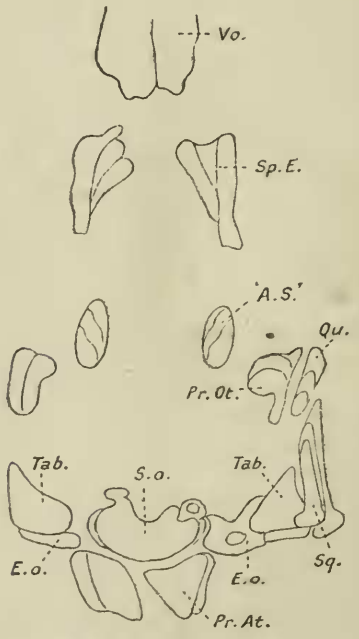
Fig. 4.



Transverse sections of skull of *Lysorophus*, to show the sphenethmoid and "alisphenoid" bones.

A. Sphenethmoid: *Fr.*, frontal; *Pa.S.*, parasphenoid; *P.Fr.*, prefrontal; *Pt.*, pterygoid; *Sp.E.*, sphenethmoid. B. "Alisphenoid" (*'A.S.'*): *Art.*, articulare of lower jaw; *Pa.*, parietal; *Qu.*, quadrate.

Fig. 5.



Three horizontal sections superposed.

Vo., vomers; *Pr.Ot.*, pro-otic; *Sq.*, squamosal; *S.o.*, supra-occipital; *E.o.*, exoccipital; *Tab.*, tabulare; *Pr.At.*, pro-atlas.